# Adjustment of egg laying by both hosts and intraspecific brood parasites in a beetle

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# Adjustment of egg laying by both hosts and intraspecific brood parasites in a beetle

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## Abstract

Brood parasites lay their eggs in the nests of other females, thereby shifting the costs of offspring care onto others. Given that care is costly, potential hosts should evolve mechanisms to avoid brood parasitism. Meanwhile, brood parasites should evolve mechanisms to circumvent host defences. Here we investigate whether hosts or intraspecific brood parasites adjust their egg laying behaviour as a mechanism to reduce or increase the effectiveness of brood parasitism. We use the burying beetle *Nicrophorus vespilloides* as our study system, in which hosts and brood parasites lay their eggs in the soil around a carcass controlled by the host. To test whether females adjust their egg laying behaviour when breeding as a host or brood parasite, we used an experimental design with three treatments: hosts, where focal females bred alongside a smaller female; brood parasites, where focal females bred alongside a larger female; and controls, where focal females bred alone. We used focal females from a narrowly defined size range to control for potential effects of body size. We found that hosts delayed the start of egg laying, which may allow them to recognise brood parasitic offspring that arrive too early. Meanwhile, brood parasites laid their eggs over an extended period, which may increase the chances that their egg laying overlapped with the host. Our results suggest that adjusting egg laying behaviour is a mechanism used by both hosts and brood parasites that may contribute to the differences in reproductive success shown in prior studies.

**KEYWORDS**
burying beetle, egg laying behaviour, intraspecific brood parasitism, reproductive tactics

## 1 | INTRODUCTION

Brood parasitism is a reproductive strategy found in some egg laying animals, where brood parasitic females avoid the costs of providing care for their offspring by laying their eggs in the nests of other females (i.e. hosts) (Andersson, 1984). Most prior work has focused on interspecific brood parasitism, where hosts and parasites are opponents in a coevolutionary arms race (Davies et al., 1989; Langmore et al., 2003; Rothstein, 1990). Intraspecific brood parasitism (also termed conspecific brood parasitism or egg dumping) is less well studied and is used by females either to supplement their own reproduction (Valpine & Eadie, 2008) or as an alternative strategy when independent reproduction is not possible (Lyon, 1993; Riehl & Strong, 2019; Yom-Tov, 1980; Zink, 2003). Prior work has mainly

focused on determining why and when females breed as intraspecific brood parasites (Andersson & Åhlund, 2000; Jaatinen et al., 2011; Lyon & Eadie, 2017; Pöysä & Pesonen, 2007; Zink, 2000). However, less attention has been paid to the potential mechanisms used by individuals breeding as either hosts or intraspecific brood parasites to reduce or increase the effectiveness of brood parasitism (but see e.g. Lemons & Sedinger, 2011; Lyon, 2003, 2007). Hosts pay substantial fitness costs from rearing unrelated offspring, and potential hosts should therefore evolve mechanisms to avoid brood parasitism (Lyon et al., 2002). Meanwhile, brood parasites obtain reproductive success without incurring costs of parental care (Åhlund & Andersson, 2001; Brown & Brown, 1998; Tallamy & Horton, 1990), and should therefore evolve mechanisms that circumvent host defences (Davies & Brooke, 1988).

One mechanism by which hosts can avoid brood parasitism is to recognise and reject brood parasitic eggs based on their appearance (Davies & Brooke, 1989; Lahti, 2006; Soler et al., 2011, 2014; Takasu, 2017), a defence that brood parasites can overcome through egg mimicry (Brooke & Davies, 1988; Lyon, 2007). However, recognition based on egg appearance carries the risk that hosts mistakenly reject some of their own eggs (Davies et al., 1996). Thus, an alternative mechanism that may minimise the effectiveness of brood parasitism is to adjust the pattern of egg laying. For instance, adjusting the start or duration of egg laying may allow hosts to reject brood parasitic eggs that appear before their own (Elwood, 1994; Müller & Eggert, 1990; Sealy, 1995; Stouffer et al., 1987). Furthermore, hosts may be able to bias the allocation of care away from brood parasitic offspring by adjusting egg laying so that the host's eggs hatch before the brood parasite's, thereby allowing host offspring to outcompete brood parasitic offspring for access to resources (Fraga, 1985; Shizuka & Lyon, 2010; Weatherhead, 1989). Brood parasites may also adjust their egg laying as a mechanism to overcome host defences. For instance, by extending the duration of egg laying, brood parasites could ensure that their egg laying overlaps with that of the host, thereby increasing the chances that some of their offspring are accepted by the host and not outcompeted by the host's offspring. Furthermore, both hosts and brood parasites may increase their own reproductive success by laying more eggs (Schmaltz et al., 2008), or larger eggs that hatch into more competitive offspring (Forbes & Wiebe, 2010; Styrsky et al., 1999). However, it is currently unclear to what extent hosts and brood parasites adjust their egg laying behaviour in ways that may influence the effectiveness of brood parasitism.

Here we examine whether females adjust their egg laying behaviour when breeding as either a host or brood parasite in the burying beetle *Nicrophorus vespilloides*. This species breeds on small vertebrate carcasses (Scott, 1998) and is well-suited for investigating egg laying in the context of intraspecific brood parasitism. Firstly, females breed in a variety of contexts, including breeding alone or assisted by a male, breeding in brood parasitic associations, or breeding communally with other females (Eggert & Müller, 1992; Müller et al., 1990a). Brood parasitism occurs frequently in this species; a study using carcasses placed in the wild found that 21 out of 42 broods had some brood parasitic larvae (Müller et al., 2007). Secondly, hosts raise fewer larvae when breeding alongside a brood parasite (Müller et al., 1990a). Hosts suppress the reproduction of brood parasites by restricting their access to carrion (Eggert et al., 2008) and selectively culling brood parasitic larvae that hatch too early (Eggert & Müller, 2011). As a result, brood parasitism is associated with strong reproductive skew in favour of the host (Eggert & Müller, 2011; Müller et al., 1990a, 2007). Yet, such broods often contain a small number of parasitic larvae both in the lab (Müller et al., 1990a) and the wild (Müller et al., 2007), suggesting that brood parasites bypass host defences. Although brood parasites produce a small numbers of larvae compared to hosts (Müller et al., 1990a), it represents an important alternative reproductive tactic in this species. Carcasses required for reproduction are rare, ephemeral, and fiercely contested and brood parasitism allows subordinate females that are excluded from raising their own brood on a given carcass by a dominant female to achieve some reproductive success before leaving to search for another breeding opportunity. Thirdly, brood parasitic associations can be generated experimentally by ensuring a difference in size between females. Larger females typically become the dominant that monopolises the carcass and provides care for the brood (Bartlett & Ashworth, 1988; Otronen, 1988; Safryn & Scott, 2000). Smaller females often act as subordinate brood parasites, laying eggs but not contributing towards care (Müller et al., 1990a). Females may breed communally, with each female providing care, but only if females are similar in size and the carcass is sufficiently large (Eggert & Müller, 1992; Komdeur et al., 2013; Richardson & Smiseth, 2020). Finally, egg laying is straightforward to record using scanners as females lay their eggs in the soil surrounding the carcass (Ford & Smiseth, 2016). Furthermore, the eggs of different females can be identified using dyes (Richardson & Smiseth, 2020; Scott, 1997).

We investigated egg laying as a mechanism used by host and brood parasite females, using an experimental design with three treatments, focal females breeding as hosts alongside a smaller female, focal females breeding as brood parasites alongside a larger female and focal females breeding alone as controls. We used focal females from a narrowly defined size range to control for potential confounding effects of body size. We recorded the start of egg laying, its duration (laying spread), the extent to which laying was skewed towards earlier in the laying period (laying skew), clutch size and egg size for each female. Burying beetles cannot recognise their own offspring after hatching (Müller & Eggert, 1990; Oldekop et al., 2007), but will kill any larvae that arrive before their own eggs hatch (Müller & Eggert, 1990). Furthermore, brood parasitic larvae that hatch after the host has completed its egg laying will be outcompeted by the host's larvae (Smiseth et al., 2007a). Therefore, if hosts adjust their egg laying in the context of intraspecific brood parasitism, we predicted they would delay the beginning of egg laying and reduce laying spread. This is because doing so would shorten the window during which brood parasitic offspring could successfully infiltrate the brood, thereby allowing hosts to attain the high levels of reproductive skew reported in prior studies (Eggert & Müller, 2011;

Müller et al., 1990a, 2007). In contrast, we predicted that brood parasites would increase laying spread because this raises the chances that at least *some* larvae hatch at the right time to avoid infanticide by the host whilst still being able to compete with the host's larvae, thereby providing a mechanism for some brood parasite larvae to infiltrate the host's brood as reported in prior studies (Müller et al., 1990a, 2007).

## 2 | METHODS

### 2.1 | Beetle husbandry

We used beetles from an outbred laboratory population descending from wild-caught individuals collected at Blackford Hill, Edinburgh. The laboratory population was maintained at 20°C under a 16L:8D photoperiod. We housed non-breeding adults in individual containers (12 × 8 × 2 cm) filled with moist soil and feed them organic beef twice weekly.

### 2.2 | Experimental procedures

Our study examined egg laying behaviour of female burying beetles in the context of intraspecific brood parasitism. We used an experimental design with three treatments, focal females breeding as hosts alongside a smaller female, focal females breeding as brood parasites alongside a larger female and focal females breeding alone. We used focal females from a narrowly defined size range and induced them to breed as either a host or a brood parasite by varying the size of the other female. This design controlled for any confounding effects of the focal female's own body size on egg laying.

We selected sexually mature females aged 10–24 days post-eclosion for use in our experiment. We measured the pronotum width of each female and then selected females with a pronotum width between 4.52 and 5.52 mm for use as focal females (mean ± SE pronotum width of focal females: 5.16 ± 0.03 mm). These focal females were assigned to one of three treatments: hosts, where the focal females bred alongside a smaller female ($n$ = 27), brood parasites, where the focal females bred alongside a larger female ($n$ = 26) and controls, where focal females bred alone ($n$ = 22). In the first two treatments, the focal female was either 10%–15% larger or 10%–15% smaller than the other female (mean ± SE pronotum width of other females when focal female was smaller: 5.59 ± 0.03 mm; mean ± SE pronotum width of other females when focal female was larger: 4.65 ± 0.05 mm). We also ensured that the two focal females in a given trial were unrelated to each other.

To identify which female laid which eggs, we fed all females beef mince containing one of two different fat-soluble dyes: Rhodamine B (Sigma-Aldrich) or Sudan Black (Fisher Scientific Ltd.) mixed in a ratio of 0.02 g of dye per 1 g of beef. Dyes are incorporated into the eggs during egg laying, making females lay pink or blue eggs respectively (Figure 1; Scott, 1997). We randomly assigned focal females to be fed a dye and ensured that the other female in a given trial was fed the other dye. We also randomly assigned control females to be fed one of the two dyes.

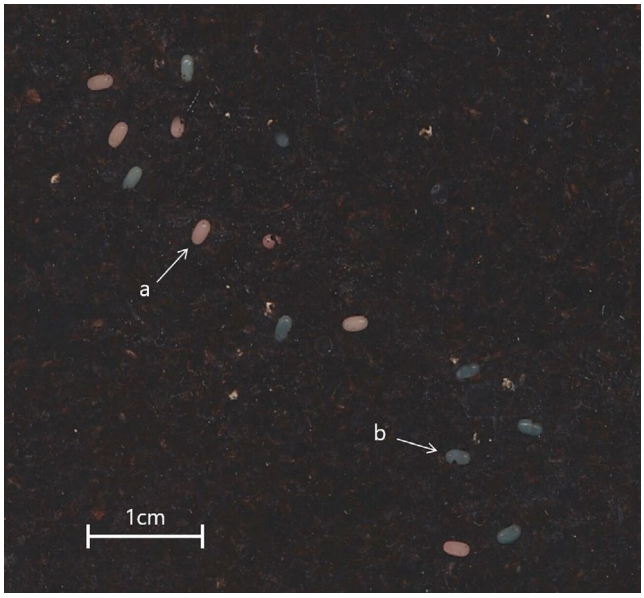


**FIGURE 1** Eggs laid by female *Nicrophorus vespilloides* after feeding on either Rhodamine B dye (pink eggs, example indicated with 'a') or Sudan Black dye (blue eggs, example indicated with 'b')

Once females had been fed dyed beef for a week, we mated them with an unrelated male from the stock population. We left each female and her mate together in a container (11 × 11 × 3 cm) lined with moist soil for 24 hours to ensure that all females received sufficient sperm for fertilising their eggs, allowing them to breed once provided with a carcass (Botterill-James et al., 2017). After mating, we weighed each female so that we could calculate her mass change after breeding (see below). To initiate breeding, we transferred females to larger containers (28 × 16 × 10 cm) lined with moist soil and containing a freshly thawed mouse carcass (Livefoods Direct Ltd.). At this time, we discarded all males to remove any potential confounding effects of male presence. In the experimental treatments with two females, we placed both females in the container at the same time, in opposite corners of the container and equidistant from the carcass. We used carcasses that weighed between 10 and 15 g (mean ± SE: 13.51 ± 0.13 g), which is within the size range used by this species (1–40 g; Müller et al., 1990b). We used relatively small carcasses to ensure that only one female became the dominant, since females can potentially breed communally on larger carcasses (>25 g) (Eggert & Müller, 1992; Komdeur et al., 2013). We were able to individually identify each female based on differences in body size and their colour, because the elytra of females that had been feeding on beef dyed with Rhodamine B had a distinct pink (rather than orange) colour. Nevertheless, in order to ensure accurate identification, we also marked all females with either one or two small spots of correction fluid on their elytra. This method of marking beetles is long-lasting, non-toxic and has no effect on their behaviour (Hagler & Jackson, 2001; Richardson & Smiseth, 2017). We ensured that

females assigned to the control treatment were also marked in the same way by randomly providing control females with either one or two small spots of correction fluid on their elytra.

We recorded the position of each female relative to the carcass three times per day for the first 2 days after they were provided with a carcass. We used this information to confirm that the larger female was a dominant host, and that the smaller female was a subordinate brood parasite. We considered a female to be dominant if she was present on or near the carcass for more observations than the other female. As anticipated, in 47 out of 53 cases, the larger female was dominant. There were no cases where both females were present on or near the carcass for an equal number of observations or where neither female was recorded on or near the carcass. We excluded the six cases in which, contrary to our expectations, the smaller female was dominant ($n$ = 2 for focal female destined to be a brood parasite, $n$ = 4 for focal female destined to be a host). We did this to avoid introducing body size as a confounding factor in our analyses. However, in five out of six of these cases only one female laid eggs, meaning that these cases were excluded from our analyses anyway (see below). We carried out similar observations on control females as a reference point for the position of breeding females in the absence of brood parasitism.

We recorded the egg laying of each female by scanning the bottom of each container every hour until the completion of egg laying using flat-bed scanners (Canon CanoScan 9000F Mark II; Canon Inc.) and VueScan professional edition software (Hamrick Software) (Ford et al., 2018; Ford & Smiseth, 2016, 2017). Eggs are visible in the soil through the bottom of the container and the visible number of eggs is strongly correlated with the actual clutch size (Monteith et al., 2012). From each scanned image, we counted the number of new eggs laid each hour, using this information to determine: (1) the start of egg laying (i.e. the time elapsed since the female had been provided a carcass until she laid her first egg), (2) laying spread (i.e. the time between the first and last egg being laid; Smiseth et al., 2006) and (3) laying skew (i.e. the extent to which laying is skewed towards earlier in the laying period; Ford & Smiseth, 2016). We calculated laying skew as $\Sigma\left(\frac{t_i - t_m}{t_m}\right) \times p_i$, where $t_i$ is the time interval in relation to the start of the laying period, $t_m$ is the middle of the laying period and $p_i$ is the proportion of the total clutch that is laid in a given time interval.

For each female, we also recorded her clutch size and measured the size of three randomly chosen eggs using ImageJ (https://imagej.nih.gov/ij/). For each egg, we measured its length and width in pixels three times and converted these measures to metric length (mm). We then calculated a prolate spheroid volume ($V$) for each egg as $V = (1/6)\,\pi w^2 L$, where $w$ is width and $L$ the length of the egg (Berrigan, 1991). We excluded an additional five broods because the eggs of either one or both females failed to hatch ($n$ = 4 for focal female destined to be a host; $n$ = 1 for focal female destined to be a brood parasite; $n$ = 0 for control females). This yielded a final sample size of $n$ = 19 for hosts, $n$ = 23 for brood parasites and $n$ = 22 for controls. We measured egg laying traits blind as to which female was the host or the brood parasite.

We left females until their larvae dispersed from the carcass approximately 7 days later. Our experimental design did not allow us to determine which larvae were produced by the host or the brood parasite. Therefore, we recorded the number and total mass of dispersing larvae for the brood as a whole. For each brood, we calculated mean larval mass by dividing the total brood mass by the number of larvae in the brood. We also weighed each female at dispersal to measure her post-breeding mass and subtracted her pre-breeding mass from this value to calculate mass change during breeding.

Our study adheres to the ASAB/ABS Guidelines for the Use of Animals in Research, the legal requirements of the UK, and all institutional guidelines at The University of Edinburgh.

### 2.3 | Statistical analyses

We analysed our data using R, version 4.0.3 (R Core Team, 2020). We used general linear models for traits with normally distributed errors (laying spread, laying skew, egg size, female mass change, brood size and mean larval mass) and a generalised linear model for one trait that had Poisson errors (clutch size). All models included the treatment of the focal female (host, brood parasite and control) as a fixed effect. We included carcass size as a covariate in all models to control for any potential effects of variation in resource size. We included clutch size as an additional covariate in analyses of laying spread and laying skew to control for any effects of clutch size on egg laying patterns. Given that our experimental design does not allow us to determine which larvae belong to the host or the brood parasite, we analysed data on brood size and mean larval mass for broods as a whole.

Focal females could potentially adjust their egg laying behaviour in two ways: by responding to the reproductive context (i.e. the presence and size of the other female) or by responding to the egg laying behaviour of the other female – for example, by starting to lay their eggs when the other female starts to lay her eggs. Prior work suggests that burying beetles are unable to tell when their competitor has laid eggs (Eggert & Müller, 2011). To confirm this was the case in our study, we re-ran the same models for egg laying behaviour described above but this time including the relevant egg laying trait of the non-focal female as an additional covariate. If, as expected, females respond to the reproductive context rather than the egg laying behaviour of their competitor, we predicted that including information on the non-focal female's egg laying would have no effect on the egg laying patterns of focal females.

## 3 | RESULTS

### 3.1 | Observations of time spent on or near the carcass

As expected, focal hosts were observed on or near the carcass more often than focal brood parasites in the first 2 days after they were provided with a carcass (estimate ± SE = 3.95 ± 0.44, $t$ = 9.06,

$p < .001$; mean counts ± SE for focal hosts = 4.29 ± 0.40; mean counts ± SE for focal brood parasites = 0.36 ± 0.15). Control females were observed on or near the carcass on more occasions than focal brood parasites (estimate ± SE = 4.42 ± 0.45, $t = 9.63$, $p < .001$; mean counts ± SE for controls = 4.77 ± 0.35), but there was no difference between control females and focal hosts in the number of times they were observed on or near the carcass (estimate ± SE = 0.48 ± 0.45, $t = 1.05$, $p = .55$).

### 3.2 | Egg laying

Hosts took longer to start egg laying than controls or brood parasites (Table 1; Figure 2A). On average, hosts delayed the onset of egg laying by 27.3% compared to controls and 29.2% compared to brood parasites. There was no difference in the time until the start of egg laying between controls and brood parasites (Table 1; Figure 2A). Brood parasites extended their laying spread compared to hosts and controls (Table 1; Figure 2B), but there was no difference in laying spread between hosts and controls (Table 1; Figure 2B). On average, brood parasites had a laying spread that was 101.3% larger than hosts and 113.7% larger than controls (Figure 2B). There was no difference in laying skew between controls, hosts or brood parasites (Table 1).

Brood parasites laid fewer eggs than either controls or hosts (Table 1; Figure 2C). Brood parasites laid, on average, 17.4% fewer eggs than controls and 18.2% fewer eggs than hosts. The number of eggs laid did not differ significantly between controls and hosts (Table 1; Figure 2C). Females laid more eggs on larger carcasses (Table 1). There was no difference in the size of eggs laid by controls, hosts or brood parasites (Table 1). Finally, as expected, including information on the egg laying behaviour of the non-focal female had no effect on egg laying of focal hosts or brood parasites (Table S1), confirming that females did not respond to the egg laying behaviour of each other.

### 3.3 | Female mass change

There was no difference in the pre-breeding mass of females assigned to the different treatments ($F_{2,59} = 1.07$, $p = .34$; mean for controls ± SE = 0.20 ± 0.0068 g; mean for hosts ± SE = 0.19 ± 0.0073 g; mean for brood parasites ± SE = 0.20 ± 0.0086 g). Brood parasites gained less mass during breeding than controls or hosts (Table 1; Figure 3), while there was no difference in mass gain between controls and hosts (Table 1; Figure 3).

### 3.4 | Brood size and mean larval mass

Broods of control females contained more larvae at dispersal than broods where the focal female was a host (estimate ± SE = −7.44 ± 1.63, $t = -4.55$, $p < .001$) or a brood parasite (estimate ± SE = −8.00 ± 1.56, $t = -5.12$, $p < .001$). There was no difference in brood size between broods where the focal female was a host or a brood parasite (estimate ± SE = 0.56 ± 1.55, $t = 0.36$, $p = .93$). On average, broods of control females were 50.4% and 45.7% larger than broods where the focal female was a host or a brood parasite respectively (Figure 4). Carcass size had no effect on brood size (estimate ± SE = 0.066 ± 0.54, $t = 0.12$, $p = .90$). Mean larval mass did not differ between broods of controls and broods where the focal female was a host (estimate ± SE = 0.0091 ± 0.0099, $t = 0.92$, $p = .63$) or a brood parasite (estimate ± SE = 0.0038 ± 0.0095, $t = 0.40$, $p = .92$). Similarly, there was no difference in mean larval mass between broods where the focal female was a host or a brood parasite (estimate ± SE = 0.0053 ± 0.0094, $t = 0.56$, $p = .84$). Finally, carcass size had no effect on mean larval mass (estimate ± SE = −0.0045 ± 0.0033, $t = -1.4$, $p = .17$).

## 4 | DISCUSSION

We investigated egg laying behaviour in the context of intraspecific brood parasitism in the burying beetle *Nicrophorus vespilloides*. We found that females acting as hosts delayed the start of egg laying. Meanwhile, females acting as brood parasites laid their eggs over an extended period, but laid fewer eggs and gained less mass than hosts or controls. Contrary to our prediction, hosts did not reduce laying spread. Furthermore, we found that control females reared more larvae than females breeding in brood parasitic associations. Below, we provide a more detailed discussion of our results and their wider implications for our understanding of the mechanisms used by hosts and intraspecific brood parasites.

Our first main finding was that hosts delayed the start of egg laying compared to brood parasites and controls. Female *N. vespilloides* cannot directly discriminate between their own and unrelated larvae (Müller & Eggert, 1990; Oldekop et al., 2007). Instead, they use temporal cues of kin discrimination, killing larvae that arrive before their own eggs are expected to hatch (Müller & Eggert, 1990). Thus, by delaying the start of egg laying, hosts likely increase the number of brood parasitic larvae that arrive too early, thereby providing a mechanism for eliminating brood parasitic larvae. Indeed, prior work in this species has shown that the portion of brood parasitic larvae killed by the host increases when the brood parasite begins laying earlier than the host (Eggert & Müller, 2011). Alternatively, hosts may delay egg laying because they have to spend time fighting for control of the carcass. However, this explanation seems unlikely given that brood parasites did not delay the onset of egg laying (Figure 2) despite having engaged in just as many fights as hosts. Furthermore, prior work shows that contests between different-sized females are typically decided in a matter of seconds (Müller et al., 1990a). Subordinate females may make forays to the carcass, but they will quickly retreat when challenged by the dominant (Müller et al., 1990a). Thus, it seems unlikely that delayed egg laying occurred because of a trade-off between egg laying and carcass defence. Instead, delaying egg laying is likely a mechanism for eliminating

**TABLE 1** Effects of focal female treatment (control, host and brood parasite) on egg laying traits and female mass change during breeding

| | | | | Brood parasite vs. control | | | Host vs. control | | | Host vs. brood parasite | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|
| **Trait** | | ***F*/LR $\chi^2$** | ***p*** | **Est (±SE)** | ***t*/*z*** | ***p*** | **Est (±SE)** | ***t*/*z*** | ***p*** | **Est (±SE)** | ***t*/*z*** | ***p*** |
| Time until first egg (h) | Treatment | $F_{2,58} = 6.69$ | **.0024** | −2.19 (2.56) | $t = -0.85$ | .67 | 6.92 (2.68) | $t = 2.57$ | **.032** | 9.11 (2.55) | $t = 3.56$ | **.0022** |
| | Carcass size (g) | $F_{1,58} = 0.062$ | .80 | — | — | — | — | — | — | — | — | — |
| Laying spread (h) | Treatment | $F_{2,57} = 14.96$ | **<.001** | 35.5 (7.37) | $t = 4.81$ | **<.001** | 1.73 (7.55) | $t = 0.23$ | .97 | −33.8 (7.37) | $t = -4.57$ | **<.001** |
| | Carcass size (g) | $F_{1,57} = 0.22$ | .64 | — | — | — | — | — | — | — | — | — |
| | Clutch size | $F_{1,57} = 0.72$ | .39 | — | — | — | — | — | — | — | — | — |
| Laying skew | Treatment | $F_{2,57} = 0.35$ | .70 | −0.020 (0.10) | $t = -0.19$ | .98 | 0.065 (0.10) | $t = 0.61$ | .82 | 0.085 (0.10) | $t = 0.81$ | .69 |
| | Carcass size (g) | $F_{1,57} = 0.24$ | .62 | — | — | — | — | — | — | — | — | — |
| | Clutch size | $F_{1,57} = 0.56$ | .45 | — | — | — | — | — | — | — | — | — |
| Clutch size | Treatment | LR $\chi^2_{2,58} = 9.31$ | **.0094** | −0.15 (0.063) | $z = -2.48$ | **.039** | 0.015 (0.063) | $z = 0.24$ | .96 | 0.17 (0.063) | $t = 2.72$ | **.019** |
| | Carcass size (g) | LR $\chi^2_{1,58} = 9.07$ | **.0025** | — | — | — | — | — | — | — | — | — |
| Egg size ($mm^3$) | Treatment | $F_{2,57} = 0.75$ | .47 | −0.11 (0.094) | $t = -1.22$ | .44 | −0.052 (0.10) | $t = -0.52$ | .86 | 0.062 (0.095) | $t = 0.65$ | .79 |
| | Carcass size (g) | $F_{1,57} = 0.063$ | .80 | — | — | — | — | — | — | — | — | — |
| Female mass change (g) | Treatment | $F_{2,58} = 17.99$ | **<.001** | −0.055 (0.011) | $t = -5.04$ | **<.001** | 0.001 (0.011) | $t = 0.10$ | .92 | 0.056 (0.011) | $t = 5.17$ | **<.001** |
| | Carcass size (g) | $F_{1,58} = 1.35$ | .24 | — | — | — | — | — | — | — | — | — |

*Note:* For normally distributed traits we provide *F* values from linear models and for Poisson distributed traits we provide likelihood ratio tests (LR $\chi^2$) from generalised linear models. For each trait we also provide parameter estimates (Est), standard errors (SE), test statistics (*t*/*z*) and *p*-values from Tukey post-hoc contrasts where multiple testing was accounted for using Bonferroni correction. Significant *p*-values are indicated in bold type.

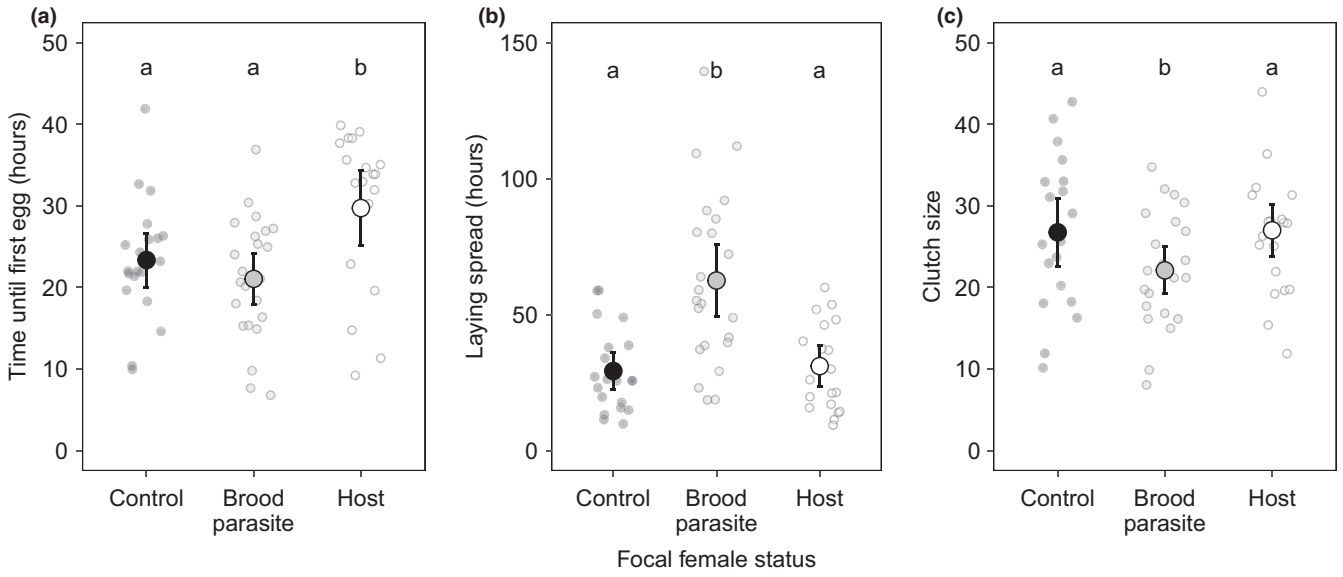


**FIGURE 2** Effects of intraspecific brood parasitism on (A) the time elapsed (hours) from being provided with a carcass until a female laid her first egg, (B) laying spread – the time (hours) between the first and last egg being laid and (C) clutch size for focal females. Black points represent control females, grey points represent brood parasites and white points represent hosts. Larger points represent means (±2 SE) whilst smaller points represent data on individual focal females. Different letters indicate statistically significant differences between treatments

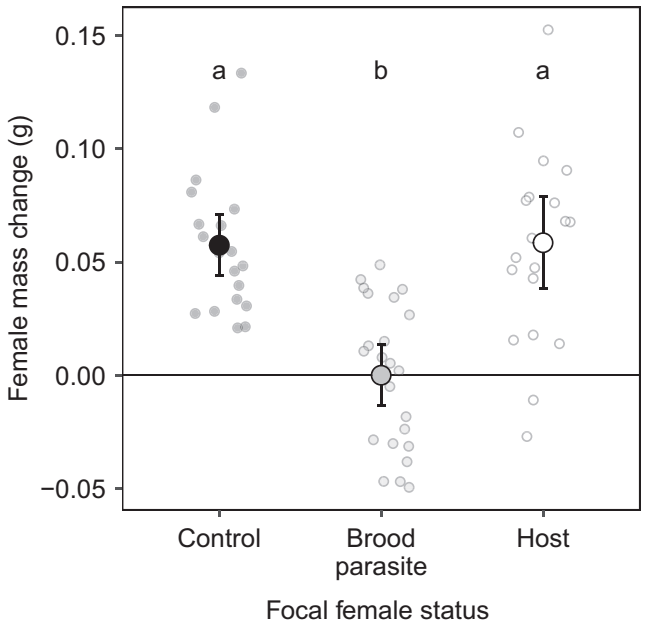


**FIGURE 3** Effects of intraspecific brood parasitism on female mass change (g) during breeding for focal females. Black points represent control females, grey points represent brood parasites, and white points represent hosts. Larger points represent means (±2 SE) whilst smaller points represent data on individual focal females. Different letters indicate statistically significant differences between treatments

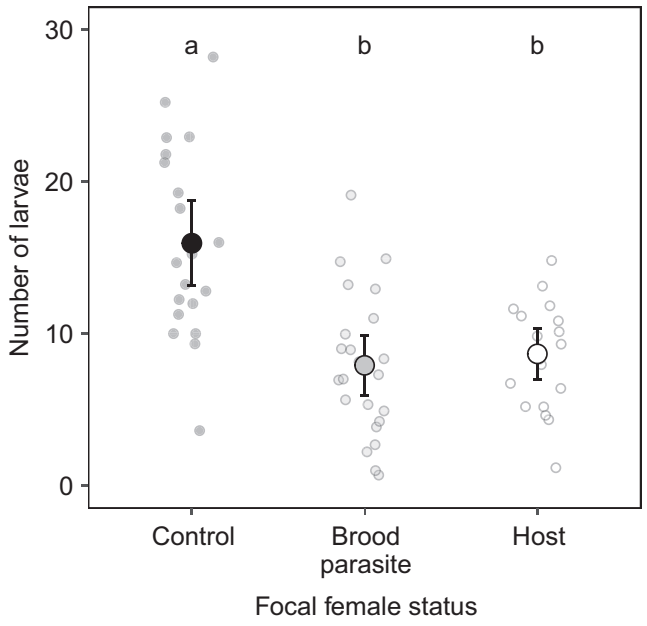


**FIGURE 4** Effects of intraspecific brood parasitism on the total number of larvae in the brood at dispersal. Black points represent broods reared by control focal females, grey points represent broods where the focal female was the brood parasite (and the non-focal female was the host) and white points represent broods where the focal female was the host (and the non-focal female was a brood parasite). Larger points represent means (±2 SE) whilst smaller points represent data on individual broods. Different letters indicate statistically significant differences between treatments

brood parasitic larvae. This mechanism may provide hosts with an adaptive mechanism for increasing their share of maternity in the brood. In support of this, prior work shows that hosts achieve higher levels of reproductive skew when they delay egg laying relative to the brood parasite (Eggert & Müller, 2011). There may be costs of delaying oviposition such as, increased likelihood that the carcass is usurped by another female or increased decomposition of the

carcass which negatively impacts eggs and larvae (Jacobs et al., 2014; Rozen et al., 2008). However, these costs are likely to be relatively small in this case given that the mean delay by hosts in our study was only about 6 hours compared to controls (Figure 2). Thus, it seems likely that the significant benefits in terms of increased reproductive skew due to a delay of this magnitude (Eggert & Müller, 2011) outweigh any potential costs.

Our second main finding was that brood parasites spread their egg laying over a longer period than hosts or controls. We predicted that brood parasites would use this mechanism as a larger laying spread increases the likelihood that their egg laying overlaps with that of the host, thereby providing a mechanism for at least *some* brood parasitic larvae to arrive during the appropriate time window when they are accepted by the host and not outcompeted by the host's own offspring. Alternatively, the laying spread of brood parasites may be constrained by their limited access to the carcass. Female burying beetles obtain nutrients for egg production by feeding from the carcass (Wilson & Knollenberg, 1984). Given that hosts repel attempts by brood parasites to access the carcass (Müller et al., 1990a), brood parasites are likely to obtain fewer resources for egg production, which in turn may limit their ability to lay their eggs more quickly. Although we found that brood parasites gained less mass during reproduction than either hosts or controls (Figure 3), it seems unlikely that nutritional constraints alone can explain our results. This is because prior work shows that there are key differences between the egg laying behaviour of brood parasites and females that are in poor nutritional condition for other reasons. Firstly, there is no evidence that food-deprived females extend their laying spread (Richardson et al., 2019). Secondly, unlike brood parasites, food-deprived females delay the onset of egg laying to obtain sufficient nutrients from the carcass (Richardson et al., 2019). Thus, the adjustment of laying spread observed in our study is specific to brood parasitism and is unlikely to be explained by nutritional constraints. Nevertheless, reduced access to the carcass may have affected brood parasites in other ways, such as their juvenile hormone (JH) levels. JH plays an important role in regulating egg laying in *N. vespilloides* (Scott et al., 2001). Thus, reduced access to the carcass may have been associated with reduced JH levels in brood parasitic females, leading to changes in their egg laying behaviour. However, it seems unlikely that such differences could explain our results given that brood parasites did not differ from control females in other aspects of their egg laying behaviour, such as the time taken to begin oviposition (Figure 2). Thus, our results suggest that increased egg laying spread most likely represents a mechanism that allows brood parasites to get some larvae into the host's brood.

Contrary to our predictions, we found no evidence that hosts compressed their laying spread. We predicted that hosts would lay their eggs over a shorter time period because this would narrow the time window during which brood parasitic larvae could successfully infiltrate the brood. There are a number of potential explanations for why hosts did not compress their laying spread. Firstly, this strategy may be redundant if delaying the start of egg laying is sufficient to suppress the number of brood parasitic larvae that make it into the brood. In support of this, prior work suggests that delaying the start of egg laying greatly reduces the number of brood parasitic larvae in the host's brood (Eggert & Müller, 2011). Secondly, because egg laying is skewed towards earlier in the laying period (Ford & Smiseth, 2016; Smiseth et al., 2008), laying the eggs over a shorter time period may have only marginal effects on the time window during which the majority of the host's larvae actually hatch. Finally, compressing laying spread may be costly as it could reduce competitive asymmetries between early and late hatched offspring, which aid parents in adaptively matching brood size to resource availability (Takata et al., 2013). In sum, our results suggest that hosts do not compress their laying spread in the context of intraspecific brood parasitism.

Brood parasites laid fewer eggs than hosts or controls. This finding may reflect that, as discussed above, hosts prevent brood parasites from feeding from the carcass, thereby suppressing their fecundity (Müller et al., 1990a). In support of this, prior work shows that the reduced fecundity of brood parasites can be ameliorated by providing them with supplemental food (Eggert et al., 2008). Taken together, our results suggest that egg laying behaviour in brood parasites is partly driven by side-effects of interactions with the host (e.g. gaining less mass and laying fewer eggs) and partly reflects mechanisms used specifically in the context of being a brood parasite (e.g. prolonging laying spread). For example, brood parasites are excluded from the carcass by the host and this leads to direct consequences that the brood parasite cannot circumvent, such as poor access to nutrients. This is likely to explain why brood parasites gained less mass during breeding and laid fewer eggs. However, our results suggest that, within this constraint, brood parasites are able to adjust their egg laying behaviour by prolonging their laying spread. As argued above, this adjustment of laying spread could allow brood parasites to increase the chances that *some* of their larvae arrive at the right time to invade the host's brood. Therefore, adjustment of egg laying behaviour may allow intraspecific brood parasites to make the best of a bad situation. Thus, our results suggest that the egg laying behaviour of intraspecific brood parasites partly reflects side-effects imposed by the behaviour of the host and partly behavioural mechanisms employed by the brood parasite.

Control females had more larvae than pairs of females breeding in brood parasitic associations. This suggests that intraspecific brood parasitism incurs costs in our system, as found in other insects (González-Megías & Sánchez-Piñero, 2003; Tallamy & Horton, 1990) and birds (Lichtenstein & Sealy, 1998; Lyon et al., 2002). We note that our experiment provides no information on what proportion of the brood was produced by the host or brood parasite and we therefore interpret this result with caution. Prior work shows that brood parasites contribute only one to two larvae in a brood of 10–20 (Eggert & Müller, 2011; Müller et al.,. ,1990a, 2007). However, even if the brood parasite contributed very few larvae (or even none at all), we still found a cost of brood parasitism to hosts as pairs of females breeding in brood parasitic associations had fewer larvae than control females. Brood parasitism can harm host reproduction because parasitic offspring kill or outcompete host offspring (Davies, 2000; Lichtenstein & Sealy, 1998). However, this is unlikely

in our species because larvae do not engage in lethal competition (Smiseth et al., 2007b) and because parasitic larvae must be similar to the host's offspring in age, and hence competitive ability (Smiseth et al., 2003), to avoid infanticide (Eggert & Müller, 2011). Instead, this finding could reflect that hosts cull more offspring when breeding alongside a brood parasite than when breeding alone. For instance, females breeding alone will accept larvae hatching several hours before their own, whilst females breeding alongside a potential brood parasite only accept larvae that hatch once their own are expected to hatch (Eggert & Müller, 2000). Alternatively, broods may contain fewer larvae due to predation by the brood parasite. In our experiment, the brood parasite remained in the container until dispersal whereas brood parasites in the wild typically leave after laying their eggs (Müller et al., 1990a). Whilst we cannot rule out this explanation, predation by the brood parasite is unlikely to have contributed substantially to larval mortality in our study. This is because the host will defend the brood against intruders prior to dispersal (Scott, 1998). Furthermore, we removed the larvae as soon as they dispersed from the carcass, leaving little opportunity for the brood parasite to encounter larvae in the soil. Thus, the most likely cause of larval mortality, and differences in brood size between controls and brood parasitic associations, is culling by the host.

Our results advance our understanding of mechanisms used in the context of intraspecific brood parasitism by demonstrating that hosts and intraspecific brood parasites adjust different aspects of their egg laying: hosts delay the start of egg laying, whilst brood parasites extend their laying period. Our experimental design controlled for potential effects of a female's own body size. Thus, our study shows that females facultatively adjust their egg laying behaviour when breeding as a host or brood parasite rather than in response to her own size. Prior work in this species has investigated the reproductive outcomes for hosts and brood parasites. These studies find that hosts typically achieve a high level of reproductive skew (Eggert & Müller, 2011; Müller et al., 1990a, 2007), but that brood parasites are still able to achieve some reproductive success by having some of their own larvae invade the host's brood (Müller et al., 1990a, 2007). Our results add to these prior studies by demonstrating that changes in egg laying behaviour provide a plausible mechanism for these patterns: delayed oviposition allows hosts to recognise brood parasitic offspring (Eggert & Müller, 2011) whilst an extended laying spread increases the chances that at least some brood parasitic larvae make it into the brood. Future work should now build on our results by manipulating laying patterns and measuring subsequent effects on reproductive success. For example, such studies would confirm how changes in egg laying behaviour influence the reproductive success of hosts and brood parasites by manipulating the timing of arrival of host and brood parasitic larvae, and monitoring larval survival using genetic tools or marked larvae.

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## CONFLICT OF INTEREST

We have no conflict of interest.

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## REFERENCES

Åhlund, M., & Andersson, M. (2001). Female ducks can double their reproduction. *Nature*, *414*, 600–601. https://doi.org/10.1038/414600b

Andersson, M. (1984). Brood parasitism within species. In C. J. Barnard (Ed.), *Producers and scroungers* (pp. 195–228): Croom-Helm. https://doi.org/10.1007/978-1-4615-9784-1_8

Andersson, M., & Åhlund, M. (2000). Host–parasite relatedness shown by protein fingerprinting in a brood parasitic bird. *Proceedings of the National Academy of Sciences of the United States of America*, *97*, 13188–13193. https://doi.org/10.1073/pnas.220137897

Bartlett, J., & Ashworth, C. M. (1988). Brood size and fitness in *Nicrophorus vespilloides* (Coleoptera: Silphidae). *Behavioural Ecology and Sociobiology*, *22*, 429–434. https://doi.org/10.1007/BF00294981

Berrigan, D. (1991). The allometry of egg size and number in insects. *Oikos*, *60*, 313–321. https://doi.org/10.2307/3545073

Botterill-James, T., Ford, L., While, G. M., & Smiseth, P. T. (2017). Resource availability, but not polyandry, influences sibling conflict in a burying beetle *Nicrophorus vespilloides*. *Behavioural Ecology*, *28*, 1093–1100. https://doi.org/10.1093/beheco/arx073

Brooke, M. D., & Davies, N. B. (1988). Egg mimicry by cuckoos *Cuculus canorus* in relation to discrimination by hosts. *Nature*, *335*, 630–632. https://doi.org/10.1038/335630a0

Brown, C. R., & Brown, M. B. (1998). Fitness components associated with alternative reproductive tactics in cliff swallows. *Behavioral Ecology*, *9*, 158–171. https://doi.org/10.1093/beheco/9.2.158

Davies, N. B. (2000). *Cuckoos, cowbirds and other cheats*: T & AD Poyser. https://doi.org/10.5040/9781472597472

Davies, N. B., Bourke, A. F., & de Brooke, M. L. (1989). Cuckoos and parasitic ants: Interspecific brood parasitism as an evolutionary arms race. *Trends in Ecology & Evolution*, *4*, 274–278. https://doi.org/10.1016/0169-5347(89)90202-4

Davies, N. B., & Brooke, M. D. L. (1988). Cuckoos versus reed warblers: Adaptations and counteradaptations. *Animal Behaviour*, *36*, 262–284. https://doi.org/10.1016/S0003-3472(88)80269-0

Davies, N. B., & Brooke, M. D. L. (1989). An experimental study of coevolution between the cuckoo, *Cuculus canorus*, and its hosts. I. Host egg discrimination. *The Journal of Animal Ecology*, *58*, 207–224. https://doi.org/10.2307/4995

Davies, N. B., Brooke, M. D., & Kacelnik, A. (1996). Recognition errors and probability of parasitism determine whether reed warblers should accept or reject mimetic cuckoo eggs. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *263*, 925–931. https://doi.org/10.1098/rspb.1996.0137

Eggert, A.-K., & Müller, J. K. (1992). Joint breeding in female burying beetles. *Behavioural Ecology and Sociobiology*, *31*, 237–242. https://doi.org/10.1007/BF00171678

Eggert, A.-K., & Müller, J. K. (2000). Timing of oviposition and reproductive skew in cobreeding female burying beetles (*Nicrophorus*

*vespilloides*). *Behavioural Ecology*, *11*, 357–366. https://doi.org/10.1093/beheco/11.4.357

Eggert, A.-K., & Müller, J. K. (2011). Timing of oviposition enables dominant female burying beetles to destroy brood-parasitic young. *Animal Behaviour*, *82*, 1227–1233. https://doi.org/10.1016/j.anbehav.2011.09.001

Eggert, A.-K., Otte, T., & Müller, J. K. (2008). Starving the competition: A proximate cause of reproductive skew in burying beetles (*Nicrophorus vespilloides*). *Proceedings of the Royal Society B: Biological Sciences*, *275*, 2521–2528. https://doi.org/10.1098/rspb.2008.0661

Elwood, R. W. (1994). Temporal-based kinship recognition: A switch in time saves mine. *Behavioural Processes*, *33*, 15–24. https://doi.org/10.1016/0376-6357(94)90057-4

Forbes, S., & Wiebe, M. (2010). Egg size and asymmetric sibling rivalry in red-winged blackbirds. *Oecologia*, *163*, 361–372. https://doi.org/10.1007/s00442-010-1629-x

Ford, L. E., Henderson, K. J., & Smiseth, P. T. (2018). Differential effects of offspring and maternal inbreeding on egg laying and offspring performance in the burying beetle *Nicrophorus vespilloides*. *Journal of Evolutionary Biology*, *31*, 1047–1057. https://doi.org/10.1111/jeb.13285

Ford, L. E., & Smiseth, P. T. (2016). Asynchronous hatching provides females with a means for increasing male care but incurs a cost by reducing offspring fitness. *Journal of Evolutionary Biology*, *29*, 428–437. https://doi.org/10.1111/jeb.12797

Ford, L. E., & Smiseth, P. T. (2017). Asynchronous hatching in a nonavian species: a test of the hurry-up hypothesis. *Behavioural Ecology*, *28*, 899–907. https://doi.org/10.1093/beheco/arx055

Fraga, R. M. (1985). Host-parasite interactions between Chalk-browed Mockingbirds and Shiny Cowbirds. *Ornithological Monographs*, *36*, 829–844, https://doi.org/10.2307/40168319

González-Megías, A., & Sánchez-Piñero, F. (2003). Effects of brood parasitism on host reproductive success: Evidence from larval interactions among dung beetles. *Oecologia*, *134*, 195–202. https://doi.org/10.1007/s00442-002-1100-8

Hagler, J. R., & Jackson, C. G. (2001). Methods for marking insects: Current techniques and future prospects. *Annual Review of Entomology*, *46*, 511–543. https://doi.org/10.1146/annurev.ento.46.1.511

Jaatinen, K., Lehtonen, J., & Kokko, H. (2011). Strategy selection under conspecific brood parasitism: An integrative modeling approach. *Behavioral Ecology*, *22*, 144–155. https://doi.org/10.1093/beheco/arq162

Jacobs, C. G., Wang, Y., Vogel, H., Vilcinskas, A., van Der Zee, M., & Rozen, D. E. (2014). Egg survival is reduced by grave-soil microbes in the carrion beetle, Nicrophorus vespilloides. *BMC Evolutionary Biology*, *14*, 1–8. https://doi.org/10.1186/s12862-014-0208-x

Komdeur, J., Schrama, M. J., Meijer, K., Moore, A. J., & Beukeboom, L. W. (2013). Cobreeding in the burying beetle, Nicrophorus vespilloides: tolerance rather than cooperation. *Ethology*, *119*, 1138–1148. https://doi.org/10.1111/eth.12174

Lahti, D. C. (2006). Persistence of egg recognition in the absence of cuckoo brood parasitism: pattern and mechanism. *Evolution*, *60*, 157–168. https://doi.org/10.1554/05-052.1

Langmore, N. E., Hunt, S., & Kilner, R. M. (2003). Escalation of a coevolutionary arms race through host rejection of brood parasitic young. *Nature*, *422*, 157–160. https://doi.org/10.1038/nature01460

Lemons, P. R., & Sedinger, J. S. (2011). Egg size matching by an intraspecific brood parasite. *Behavioral Ecology*, *22*, 696–700. https://doi.org/10.1093/beheco/arr035

Lichtenstein, G., & Sealy, S. G. (1998). Nestling competition, rather than supernormal stimulus, explains the success of parasitic brown-headed cowbird chicks in yellow warbler nests. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *265*, 249–254. https://doi.org/10.1098/rspb.1998.0289

Lyon, B. E. (1993). Conspecific brood parasitism as a flexible female reproductive tactic in American coots. *Animal Behaviour*, *46*, 911–928. https://doi.org/10.1006/anbe.1993.1273.

Lyon, B. E. (2003). Egg recognition and counting reduce costs of avian conspecific brood parasitism. *Nature*, *422*, 495–499. https://doi.org/10.1038/nature01505

Lyon, B. (2007). Mechanism of egg recognition in defenses against conspecific brood parasitism: American coots (*Fulica americana*) know their own eggs. *Behavioral Ecology and Sociobiology*, *61*, 455–463. https://doi.org/10.1007/s00265-006-0273-2

Lyon, B. E., & Eadie, J. M. (2017). Why do birds lay eggs in conspecifics' nests? In M. Soler, (Ed.), *Avian brood parasitism*. (pp. 105–123): Springer. https://doi.org/10.1007/978-3-319-73138-4_6

Lyon, B. E., Hochachka, W. M., & Eadie, J. M. (2002). Paternity-parasitism trade-offs: A model and test of host-parasite cooperation in an avian conspecific brood parasite. *Evolution*, *56*, 1253–1266. https://doi.org/10.1111/j.0014-3820.2002.tb01436.x

Monteith, K. M., Andrews, C., & Smiseth, P. T. (2012). Post-hatching parental care masks the effects of egg size on offspring fitness: A removal experiment on burying beetles. *Journal of Evolutionary Biology*, *25*, 1815–1822. https://doi.org/10.1111/j.1420-9101.2012.02567.x

Müller, J. K., Braunisch, V., Hwang, W., & Eggert, A.-K. (2007). Alternative tactics and individual reproductive success in natural associations of the burying beetle, Nicrophorus vespilloides. *Behavioral Ecology*, *18*, 196–203. https://doi.org/10.1093/beheco/arl073

Müller, J. K., & Eggert, A.-K. (1990). Time-dependent shifts between infanticidal and parental behavior in female burying beetles a mechanism of indirect mother-offspring recognition. *Behavioral Ecology and Sociobiology*, *27*, 11–16. https://doi.org/10.1007/BF00183307

Müller, J. K., Eggert, A.-K., & Dressel, J. (1990a). Intraspecific brood parasitism in the burying beetle, *Necrophorus vespilloides* (Coleoptera: Silphidae). *Animal Behaviour*, *40*, 491–499. https://doi.org/10.1016/S0003-3472(05)80529-9

Müller, J. K., Eggert, A.-K., & Furlkröger, E. (1990b). Clutch size regulation in the burying beetle *Necrophorus vespilloides* Herbst (Coleoptera: Silphidae). *Journal of Insect Behavior*, *3*, 265–270. https://doi.org/10.1007/BF01417917

Oldekop, J. A., Smiseth, P. T., Piggins, H. D., & Moore, A. J. (2007). Adaptive switch from infanticide to parental care: How do beetles time their behaviour? *Journal of Evolutionary Biology*, *20*, 1998–2004. https://doi.org/10.1111/j.1420-9101.2007.01364.x

Otronen, M. (1988). The effect of body size on the outcome of fights in burying beetles (Nicrophorus). *Annales Zoologici Fennici*, *25*, 191–201. https://doi.org/10.1016/s0003-3472(05)81000-0

Pöysä, H., & Pesonen, M. (2007). Nest predation and the evolution of conspecific brood parasitism: From risk spreading to risk assessment. *The American Naturalist*, *169*, 94–104. https://doi.org/10.1086/509943

R Core Team. (2020). *R: A language and environment for statistical computing*: R Foundation for Statistical Computing. http://www.R-project.org/

Richardson, J., Ross, J., & Smiseth, P. T. (2019). Food deprivation affects egg laying and maternal care but not offspring performance in a beetle. *Behavioral Ecology*, *30*, 1477–1487. https://doi.org/10.1093/beheco/arz104

Richardson, J., & Smiseth, P. T. (2017). Intraspecific competition and inbreeding depression: Increased competitive effort by inbred males is costly to outbred opponents. *The American Naturalist*, *189*, 539–548. https://doi.org/10.1086/691328

Richardson, J., & Smiseth, P. T. (2020). Maternity uncertainty in cobreeding beetles: Females lay more and larger eggs and provide less care. *Behavioral Ecology*, *31*, 641–650. https://doi.org/10.1093/beheco/araa006

Riehl, C., & Strong, M. J. (2019). Social parasitism as an alternative reproductive tactic in a cooperatively breeding cuckoo. *Nature*, *567*, 96–99. https://doi.org/10.1038/s41586-019-0981-1

Rothstein, S. I. (1990). A model system for coevolution: avian brood parasitism. *Annual Review of Ecology and Systematics*, *21*, 481–508. https://doi.org/10.1146/annurev.es.21.110190.002405

Rozen, D. E., Engelmoer, D. J. P., & Smiseth, P. T. (2008). Antimicrobial strategies in burying beetles breeding on carrion. *Proceedings of the National Academy of Sciences of the United States of America*, *105*, 17890–17895. https://doi.org/10.1073/pnas.0805403105.

Safryn, S. A., & Scott, M. P. (2000). Sizing up the competition: Do burying beetles weigh or measure their opponents? *Journal of Insect Behavior*, *13*, 291–297. https://doi.org/10.1023/A:1007700601095

Schmaltz, G., Quinn, J. S., & Lentz, C. (2008). Competition and waste in the communally breeding smooth-billed ani: Effects of group size on egg-laying behaviour. *Animal Behaviour*, *76*, 153–162. https://doi.org/10.1016/j.anbehav.2007.12.018

Scott, M. P. (1997). Dominance and differential ovicide in the communally breeding burying beetle *Nicrophorus tomentosus*. *Behavioural Ecology and Sociobiology*, *40*, 313–320. https://doi.org/10.1007/s002650050347

Scott, M. P. (1998). The ecology and behavior of burying beetles. *Annual Review of Entomology*, *43*, 595–618. https://doi.org/10.1146/annurev.ento.43.1.595

Scott, M. P., Trumbo, S. T., Neese, P. A., Bailey, W. D., & Roe, R. M. (2001). Changes in biosynthesis and degradation of juvenile hormone during breeding by burying beetles: A reproductive or social role? *Journal of Insect Physiology*, *47*, 295–302. https://doi.org/10.1016/S0022-1910(00)00116-5

Sealy, S. G. (1995). Burial of cowbird eggs by parasitized yellow warblers: An empirical and experimental study. *Animal Behaviour*, *49*, 877–889. https://doi.org/10.1006/anbe.1995.0120

Shizuka, D., & Lyon, B. E. (2010). Coots use hatch order to learn to recognize and reject conspecific brood parasitic chicks. *Nature*, *463*, 223–226. https://doi.org/10.1038/nature08655.

Smiseth, P. T., Darwell, C. T., & Moore, A. J. (2003). Partial begging: an empirical model for the early evolution of offspring signalling. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *270*, 1773–1777. https://doi.org/10.1098/rspb.2003.2444

Smiseth, P. T., Hwang, W., Steiger, S., & Müller, J. K. (2008). Adaptive consequences and heritable basis of asynchronous hatching in *Nicrophorus vespilloides*. *Oikos*, *117*, 899–907. https://doi.org/10.1111/j.0030-1299.2008.16473.x

Smiseth, P. T., Lennox, L., & Moore, A. J. (2007b). Interaction between parental care and sibling competition: Parents enhance offspring growth and exacerbate sibling competition. *Evolution: International Journal of Organic Evolution*, *61*, 2331–2339. https://doi.org/10.1111/j.1558-5646.2007.00192.x

Smiseth, P. T., Ward, R. J. S., & Moore, A. J. (2006). Asynchronous hatching in *Nicrophorus vespilloides*, an insect in which parents provide food for their offspring. *Functional Ecology*, *20*, 151–156. https://doi.org/10.1111/j.1365-2435.2006.01072.x

Smiseth, P. T., Ward, R. J., & Moore, A. J. (2007a). Parents influence asymmetric sibling competition: Experimental evidence with partially dependent young. *Ecology*, *88*, 3174–3182. https://doi.org/10.1890/06-1992.1

Soler, J. J., Pérez-Contreras, T., De Neve, L., Macías-Sánchez, E., Møller, A. P., & Soler, M. (2014). Recognizing odd smells and ejection of brood parasitic eggs. An experimental test in magpies of a novel defensive trait against brood parasitism. *Journal of Evolutionary Biology*, *27*, 1265–1270. https://doi.org/10.1111/jeb.12377

Soler, M., Ruiz-Castellano, C., del Carmen, F.-P., Rösler, A., Ontanilla, J., & Pérez-Contreras, T. (2011). House sparrows selectively eject parasitic conspecific eggs and incur very low rejection costs. *Behavioral Ecology and Sociobiology*, *65*, 1997. https://doi.org/10.1007/s00265-011-1209-z

Stouffer, P. C., Kennedy, E. D., & Power, H. W. (1987). Recognition and removal of intraspecific parasite eggs by starlings. *Animal Behaviour*, *35*, 1583–1584. https://doi.org/10.1016/S0003-3472(87)80040-4

Styrsky, J. D., Eckerle, K. P., & Thompson, C. F. (1999). Fitness–related consequences of egg mass in nestling house wrens. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, *266*, 1253–1258. https://doi.org/10.1098/rspb.1999.0771

Takasu, F. (2017). Evolution and maintenance of egg rejection by hosts as adaptation against conspecific brood parasites: An individual-based model. In: M. Soler, (Ed.), *Avian brood parasitism*. (pp. 125–142): Springer. https://doi.org/10.1007/978-3-319-73138-4_7

Takata, M., Koyama, S., Satoh, T., & Fugo, H. (2013). Asynchronous hatching and brood reduction by filial cannibalism in the burying beetle *Nicrophorus quadripunctatus*. *Journal of Ethology*, *31*(3), 249–254. https://doi.org/10.1007/s10164-013-0373-1

Tallamy, D. W., & Horton, L. A. (1990). Costs and benefits of the egg-dumping alternative in *Gargaphia* lace bugs (Hemiptera: Tingidae). *Animal Behaviour*, *39*, 352–359. https://doi.org/10.1016/S0003-3472(05)80881-4

Valpine, P., & Eadie, J. M. (2008). Conspecific brood parasitism and population dynamics. *The American Naturalist*, *172*, 547–562. https://doi.org/10.1086/590956

Weatherhead, P. J. (1989). Sex ratios, host-specific reproductive success, and impact of Brown-headed Cowbirds. *The Auk*, *106*, 358–366. https://doi.org/10.1093/auk/106.3.358

Wilson, D. S., & Knollenberg, W. G. (1984). Food discrimination and ovarian development in burying beetles (Coleoptera: Silphidae: *Nicrophorus*). *Annals of the Entomological Society of America*, *77*, 165–170. https://doi.org/10.1093/aesa/77.2.165

Yom-Tov, Y. (1980). Intraspecific nest parasitism in birds. *Biological Reviews*, *55*, 93–108. https://doi.org/10.1111/j.1469-185X.1980.tb00689.x

Zink, A. G. (2000). The evolution of intraspecific brood parasitism in birds and insects. *The American Naturalist*, *155*, 395–405. https://doi.org/10.1086/303325

Zink, A. G. (2003). Intraspecific brood parasitism as a conditional reproductive tactic in the treehopper *Publilia concava*. *Behavioral Ecology and Sociobiology*, *54*, 406–415. https://doi.org/10.1007/s00265-003-0649-5

## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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